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Spatial structure in groups of spanish ibex *(Capra pyrenaica)*

C. L. ALADOS

Estación Experimental de Zonas Aridas (CSIC), General Segura, 1, Almería, 04001 (Spain).

Key words : Capra pyrenaica. Group cohesion. Spatial organization.

RESUME

Structure spatiale au sein de groupes d'Ibex d'Espagne (*Capra pyrenaica*).

Les auteurs ont étudié plusieurs aspects de la structure spatiale d'une population d'Ibex espagnol (*Capra pyrenaica*) sur une période de 6 mois (1982-1983), incluant la saison du rut (nov-dec), dans le sud-est de l'Espagne (Sierra de Cazorla y Segura). Les Ibex ont été regroupés en 9 classes selon l'âge et le sexe. La position des classes d'âge et de sexe à l'intérieur des groupes ainsi que les distances des animaux à l'intérieur de chaque groupe a varié au long de l'année. Pendant la saison du rut, les adultes mâles ont eu tendance à occuper une position centrale, les femelles se situant à la périphérie des groupes. Aux autres époques les adultes mâles de groupes mixtes ont eu tendance à se situer à la périphérie alors que les femelles n'ont montré aucune tendance particulière. La cohésion du groupe pendant le pâturage est réduite, quand la nourriture se trouve dispersée. L'Ibex d'Espagne révèle une association préférentielle entre des individus d'âge similaire ou voisin à l'exception de la période maximale de rut.

Mots clés : Capra pyrenaica. Cohesion du groupe. Structure spatiale.

SUMMARY

Some aspects of the spatial structure of a population of the Spanish ibex (*Capra pyrenaica*) were studied for a total of six months during 1982 and 1983, including the rut period (Nov-Dec), on the Sierra de Carzola y Segura in south-eastern- Spain. The ibex were put into nine age/sex classes within groups and the nearest neighbour distances were recorded. The position of animals within the group changed with the time of year. During the rut, adult males tended to be central with females on the periphery of the groups. At other times adult

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Brown R.E., Moger W.H., 1983. Hormonal correlates of parental behavior in male rats. *Horm. Behav., 17,* 356-365.

Cohen J., Bridges R.S., 1981. Retention of maternal behavior in nulliparous and primiparous rats: Effects of duration of previous maternal experience. *J. Comp. Physiol. Psychol., 95,* 450-459.

Elwood R.W., 1977. Changes in the responses of male and female gerbils (*Meriones unguiculatus*) towards test pups during the pregnancy of the female. *Anim. Behav., 25,* 46-51.

Elwood R.W., 1980. The development, inhibition and disinhibition of pup-cannibalism in the Mongolian gerbil. *Anim. Behav., 28,* 1188-1194.

Elwood R.W., Ostermeyer M.C., 1984. Does copulation inhibit infanticide in male rodents ? *Anim. Behav., 32,* 293-305.

Fleming A.S., Rosenblatt J.S., 1974. Maternal behavior in the virgin and lactating rat. *J. Comp. Physiol. Psychol., 86,* 957-972.

Gibber J.R., Piontkewitz Y., Terkel J., 1984. Response of male and female Siberian hamsters towards pups. *Behav. and Neural Biol., 42,* 177-182.

Gray P., Chesley S., 1984. Development of maternal behavior in nulliparous rats (*Rattus norvegicus*) : Effects of sex and early maternal experience. *J. Comp. Psychol., 98,* 91-99.

Jakubowski M., Terkel J., 1982. Infanticide and caretaking in non-lactating *Mus musculus* : Influence of genotype, family group and sex. *Anim. Behav., 30,* 1029-1035.

Jakubowski M., Terkel J., 1985a. Incidence of pup-killing and parental behavior in virgin female and male rats (*Rattus norvegicus*) : Differences between Wistar and Sprague-Dawley stocks. *J. Comp. Psychol., 99,* 93-97.

Jakubowski M., Terkel J., 1985b. Transition from pup-killing to parental behavior in male and virgin female albino rats. *Physiol. Behav., 34,* 683-686.

Leboucher G., Lescoat G., 1986. Réponses comportementale et surrénalienne à l'exposition brève ou chronique à des nouveau-nés chez des rats Wistar adultes. *Biol. Behav., 11,* 116-129.

Mayer A.D., Freeman N.C.G., Rosenblatt J.S., 1979. Ontogeny of maternal behavior in the laboratory rat : Factors underlying changes in responsiveness from 30 to 90 days. *Dev. Psychobiol., 12,* 425-439.

Mayer A.D., Rosenblatt J.S., 1984. Prepartum changes in maternal responsiveness and nest defense in *Rattus norvegicus, J. Comp, Psychol., 98,* 177-188.

Rosenblatt J.S., 1967. Nonhormonal basis of maternal behavior in the rat. *Science, 156,* 1512-1514.

Siegel S., 1956. *Non parametric statistics for the behavioral sciences.* N.Y. Mac Graw-Hill Ed.

Terkel J., Rosenblatt J.S., 1972. Humoral factors underlying maternal behavior at parturition : Cross transfusion between freely moving rats. *J. comp. Physiol. Psychol., 86,* 957-972.

males in mixed groups tended to be peripheral but females showed no significant tendency. Group cohesion during feeding is reduced when the food is dispersed. The Spanish ibex shows a preferential association between individuals of the same or similar age class except during the peak of rut.

INTRODUCTION

An individual's position in space potentially affects both its foraging success and its vulnerability to predators. The latter should increase with the distance from other group members and with the distance from the centre of the group (De Vore, 1965, Hamilton, 1971 Jennings & Evans, 1980). Foraging close to neighbours apparently enhances foraging success in a variety of species when the food resource is clumped in space or time (Horn, 1968, Eisenberg *et al.*, 1972, Krebs, 1973), but not when food distribution is relatively homogeneous (Goss-Custard 1976, Rabenold & Christensen, 1979). These conclusions are based on studies with birds or primates, whose food is usually much more clumped than is the case with herbivores. The spatial pattern in mammals is also partly a consequence of interindividual aggression (Walther, 1977, Robinson, 1981).

Since little is known of the spatial distribution of ungulates, a study was carried out on part of the population of Spanish ibex (*Capra pyrenaica*) in the Sierras de Cazorla y Segura in south-eastern Spain. A description of the study area is given in Alados (1985a).

METHODS

Spanish ibex forage in small groups ranging on size from 1 to 14 as average (Alados, 1985b). A group is defined here as a number of animals all of which are within 100 metres of each other. Only groups with five or more members were considered in this study in order to reduce the bias towards being peripheral in small groups.

Two positions within the group were recognized: central and peripheral. An animal was recorded as central if it was within an area circumscribed by lines joining the outlying animals in the group and as peripheral if it was not (Clutton-Brock *et al.*, 1976; Hall, 1983).

Observations were carried out between dawn and dusk from September, to December, 1983. The sampling methode used was scan sampling from a fixed point (Altmann, 1974). At each sampling point the distance to the nearest neighbour was noted for all individuals within the group. The nearest neighbour distance was taken to be the linear distance between an animal and the one nearest to it. The distance between a mother and her dependent offspring was not taken into account, but the distance between the juvenile and the nearest animal, other than its mother, was considered. Distances were estimated by eye using the known length of an adult female as a guide. Observations were made with the help of a pair of binoculars (10 × 40) or a telescope (30 × 70). In total, the data analyzed for the present paper cover 451 hours of observations.

As individual animals could not be identified, the results are given for age and sex classes based on the sizes of the body and horns. For most of the analyses only one class of female was recognized — those older than 1 year — but two classes of males : subadults 1-4 years old and adults those over 4 years of age were considered. The fourth age/sex class was kids up to one year of age. In one analysis two classes of females were considered (subadult females, 1-2 years old and adult females, older than 2 years), and six age classes of males. The latter were: class V (over 10 years old), class IV (from 8 to 10 years old), class III (from 6 to 8 years old), class II (from 4 to 6 years old), class I (from 2 to 4 years old) and (♂J).

In order to assess the possible effects of various activities on the position of the animal within its group, instantaneous scan samples were made of the activities of all members in the group at intervals of 60 minutes. In order to reduce sex bias in behaviour, only females were considered. Altogether, 642 such samples were taken. The activities recognized were: resting, feeding, walking, vigilance and social interactions (Alados, in press).

The frequency with which animals in each age/sex class were present on the periphery of the group was calculated by dividing the number so recorded by the total number of animals of the relevant age/sex class that was observed.

Analysis of the data followed Altmann & Altmann (1977) whose random model assumes that the probability of sampling from age/sex class $\underline{i}$ is the probability that an individual selected at random is in class $\underline{i}$, that is

$$P_i = m_i/\Sigma_k m_k$$

where m_i denotes the number of individuals in class $\underline{i}$. The probability that the subject's nearest neighbour is in class $\underline{j}$ is the probability that an individual selected at random is in class $\underline{j}$, that is

$$P_j = \frac{m_j}{\Sigma_k m_k - 1} \text{ if } \underline{i} \neq \underline{j} \text{ and}$$

$$P_j = \frac{m_j - 1}{\Sigma_k m_k - 1} \text{ if } \underline{i} = \underline{j}$$

The probability that the neighbour of class $\underline{i}$ will be a member of class $\underline{j}$ is $P_{i \rightarrow j} = P_i . P_j$, and thus the expected number of class—$\underline{j}$ neighbours of class—$\underline{i}$ members will be

$$E_{i \rightarrow j} = \frac{m_i}{\Sigma_k m_k} . \frac{m_j}{\Sigma_k m_k - 1} . N \text{ if } \underline{i} \neq \underline{j}$$

$$E_{i \rightarrow j} = \frac{m_j}{\Sigma_k m_k} . \frac{(m_j - 1)}{\Sigma_k m_k - 1} . N \text{ if } \underline{i} = \underline{j}$$

wher N = total number of individuals sampled. Brown's algorithm (Brown, 1974) was used to identify the significant celss in order to ascertain which association contributed most to the overall χ^2. This technique explores the effect on total χ^2 of successive cells of a contingency table and yields a list of cells ranked according to the magnitude of their effect on the overall χ^2.

An index of association (Van Hoff, 1973) between each age/sex class is Q_{ij} defined as the expected number of times that the neighbour of class $\underline{i}$ will be a member of class $\underline{j}$

$$Q_{ij} = \frac{O_{ij} - E_{ji}}{\sqrt{E_{ij}}}$$

where, O_{ij} = the observed number of times that the neighbour of class i will be class j, and E_{ij} = the expected value calculated os in a previous paragraph.

In addition to the G test, the χ^2 test and Sparman rank correlation coefficient (r_s) were used.

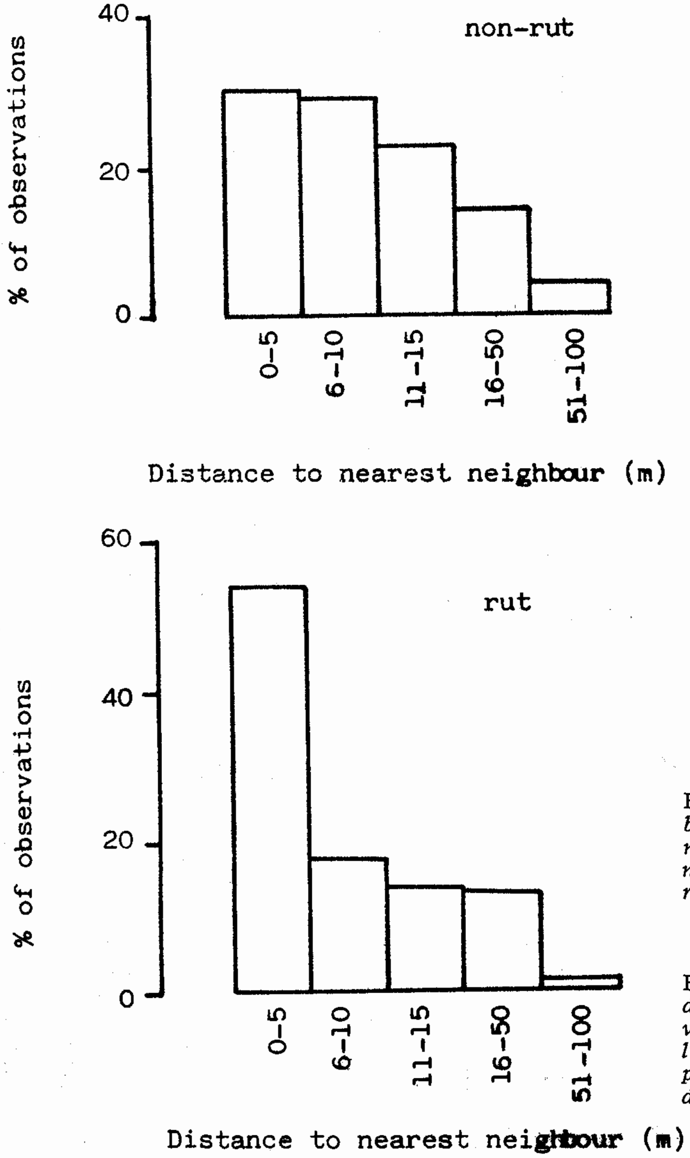

Fig. 1 : *Frequency distributions of distances to nearest neighbour in Spanish ibex before and during the rut (Sept-Dec).*

Fig. 1 : *Histogramme des distances par rapport au voisin le plus proche chez l'Ibex espagnol avant et pendant le rut (sept.-déc.).*

RESULTS

POSITION IN GROUP

Outside the rut, adult males tend to be peripheral ($\chi^2 = 4.52$, df = 1, $P < 0.05$). This observation suggests that the males, when not in rut, tend to avoid competition for food.

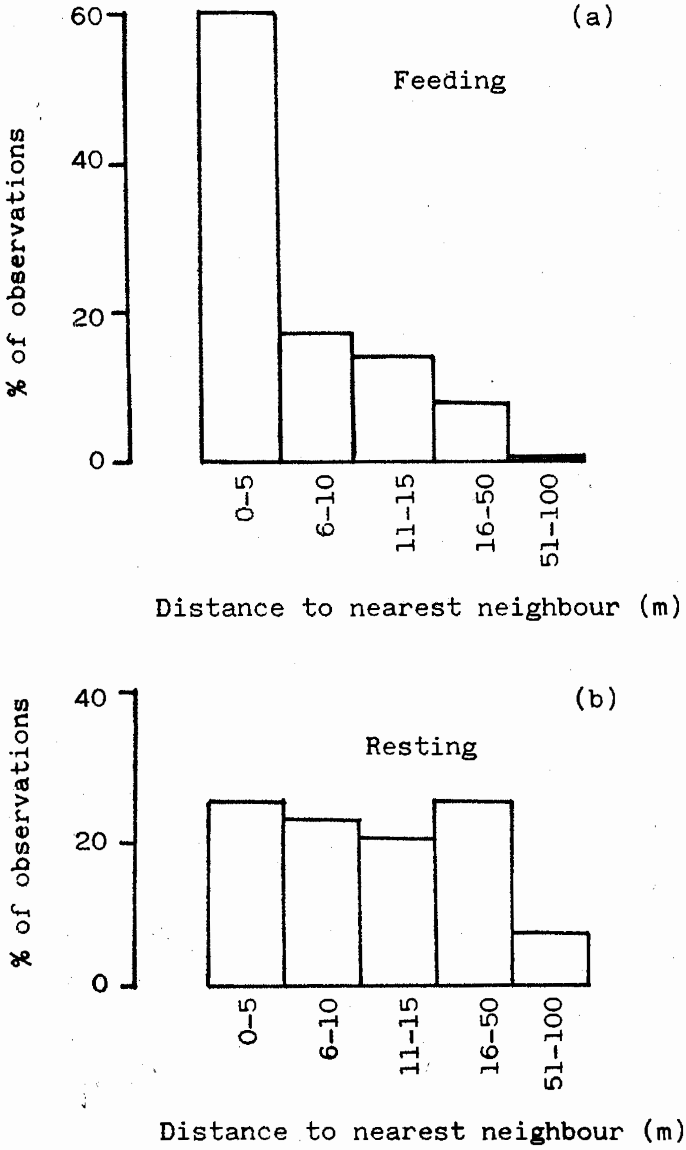

Fig. 2: *Frequency distributions of distances to nearest neighbour during the peak of the rut (1-15 Dec) for* a) *feeding and* b) *resting ibex.*

Fig. 2: *Histogramme des distances par rapport au voisin le plus proche au pic de la période du rut (1-15 déc.) pour un Ibex* a) *pâturant;* b) *au repos.*

During the rut period (Nov-Dec) the adult males tend to be located at the centre of the group ($\chi^2 = 8.49$, df = 1, $P < 0.01$), and the females on the periphery ($\chi^2 = 4.85$, df = 1, $P < 0.05$). This difference between

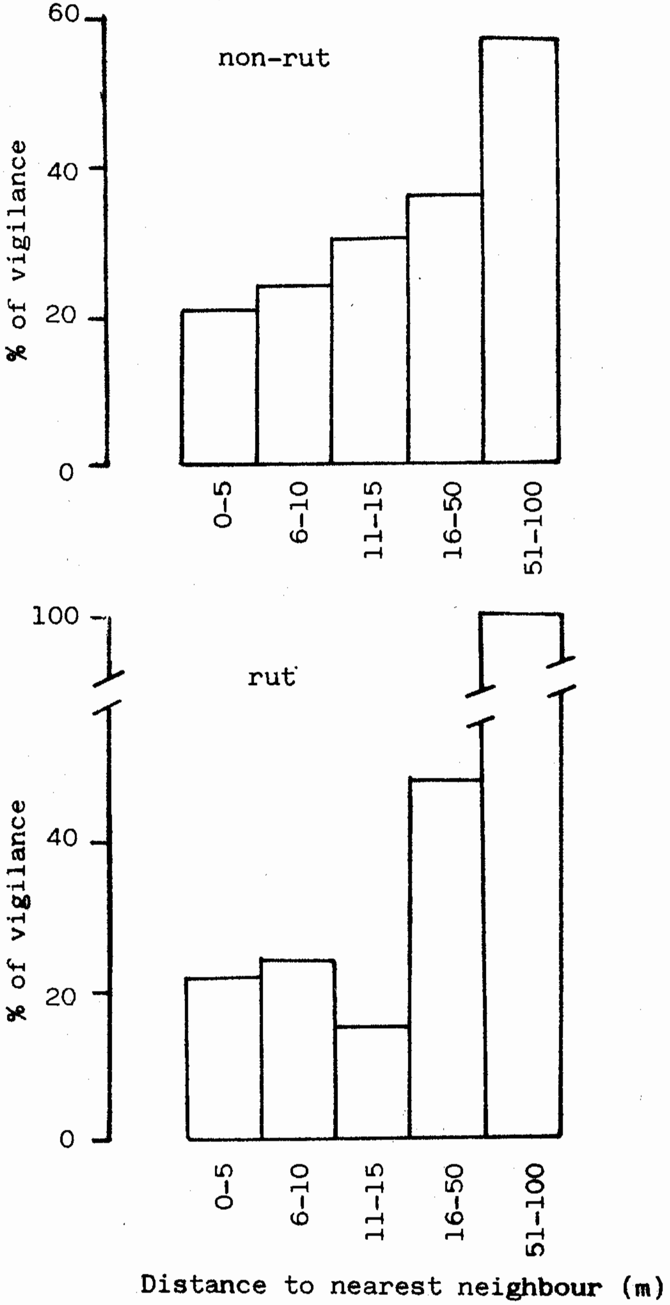

Fig. 3: *Percentage of records in which ibex were vigilant during feeding periods.*

Fig. 3: *Evaluation du pourcentage d'Ibex éveillés au cours des périodes de pâturage.*

the sexes may be due to the fact that during the rut the males show a higher tendency towards searching for mates than towards avoiding competition for food. This is also suggested by the reduced feeding activity at this time of the year (Alados, in press).

GROUP COHESION

In theory the distance to its nearest neighbour potentially affects both an animal's risk from predation and its foraging success, but during the rut there is another factor, — the need to search for mates. This should affect the cohesiveness of the group and the animals were indeed found to be closer together during the rut than at other times (G test : $G = 36.86$, $df = 4$, $P < 0.001$ two tailet test). (*fig. 1*).

The cohesiveness of the ibex was greater when the animals were feeding than when they were resting (G test : $G = 44.66$, $df = 4$, $P < 0.001$, two tailed test) (*fig. 2*).

If the amount of foraging varies with inter-individual distance, this could be a consequence of changes in the degree of vigilance. To control this effect, the number of instantaneous samples in which vigilance occurred was divided by the number of samples in which either foraging or vigilance was recorder. The results showed that vigilance on the periphery of the group was higher than in the centre. The

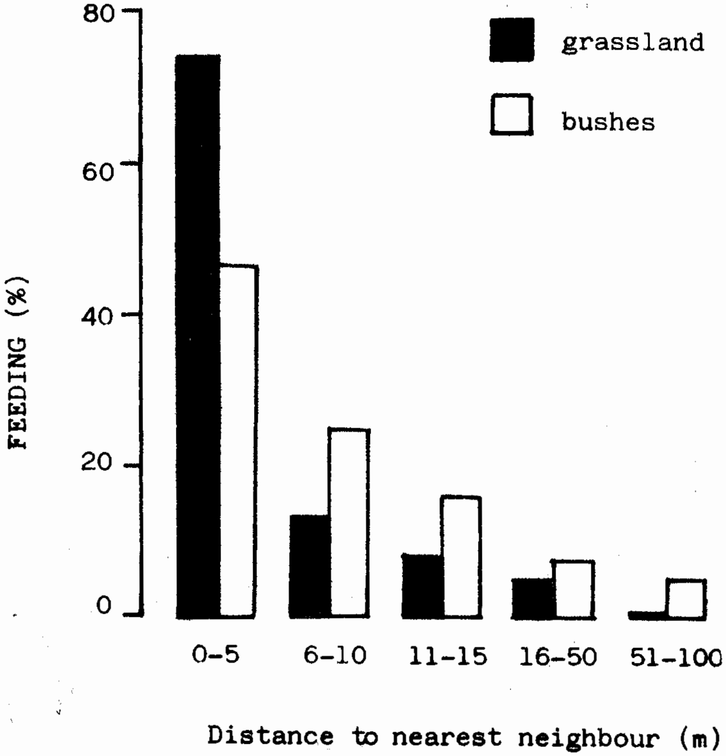

Fig. 4 : *Percentage of time spent feeding on grassland or on bushes according to distance from nearest neighbours.*

Fig. 4 : *Evaluation du pourcentage du temps passé à paître sur prairie ou sur broussaille, en fonction de la distance des voisins les plus proches.*

overall trend of decreasing vigilance with increasing proximity to another group member is significant outside the rut ($r_s = 1$, $P < 0.05$, one tailed test). This tendency is maintained during rut although it is not significant ($r_s = 0.7$, $P > 0.05$, N.S., one tailed test) (*fig. 3*).

Since competition for food should be more intense when food is dispersed rather than clumped, the nearest neighbour distance should increase as the food becomes more dispersed. In Cazorla, bushes are more dispersed than grass and, as predicted, the inter-individual distance is greater when the ibex are feeding on bushes (G test : $G = 18.98$, $df = 4$, $P < 0.001$) (*fig. 4*).

SPATIAL ORGANIZATION

The association between age/sex classes within a group was determined from the nearest neighbour association during the rut period. The relative deviations from the number of times that pairs of age/sex classes are expected to be together are shown in *fig. 5* for the pre-rut

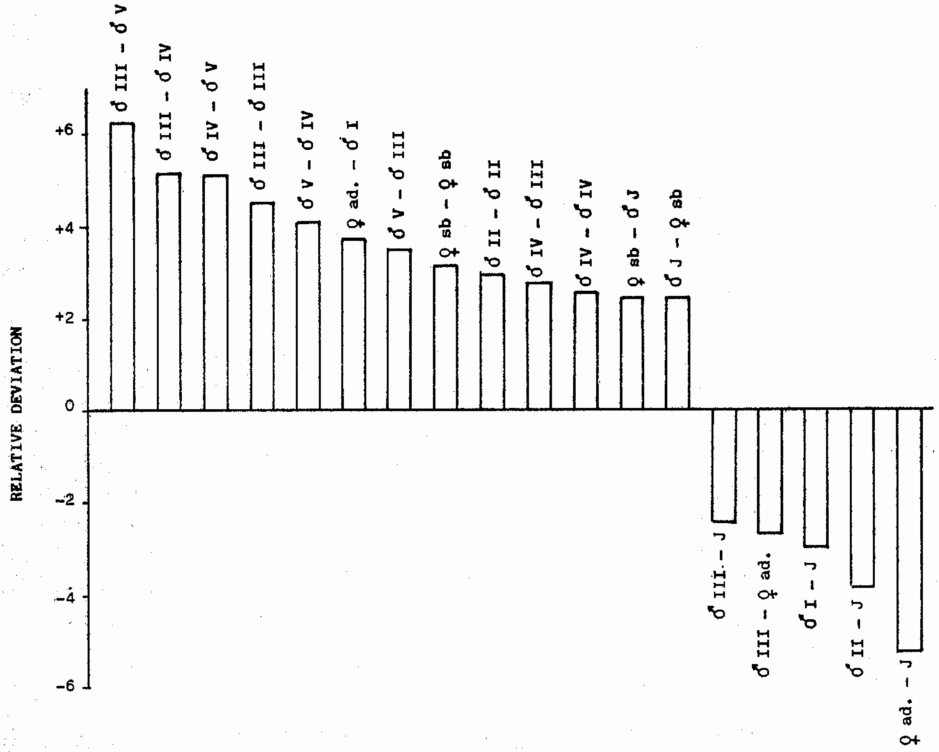

Fig. 5 : *Relative deviation (Q_{ij}) from the number of times that each pair of age/sex classes shown are expected to be together during the pre-rut period in November. All associations shown are statistically significant ($P < 0.05$).*

Fig. 5 : *Ecart relatif (Q_{ij}) par rapport au nombre de fois pour lequel chaque paire de classes d'âge et sexe devrait rester ensemble pendant la période précédant le rut (novembre). Toutes les associations présentées sont statistiquement significatives ($p < 0.05$).*

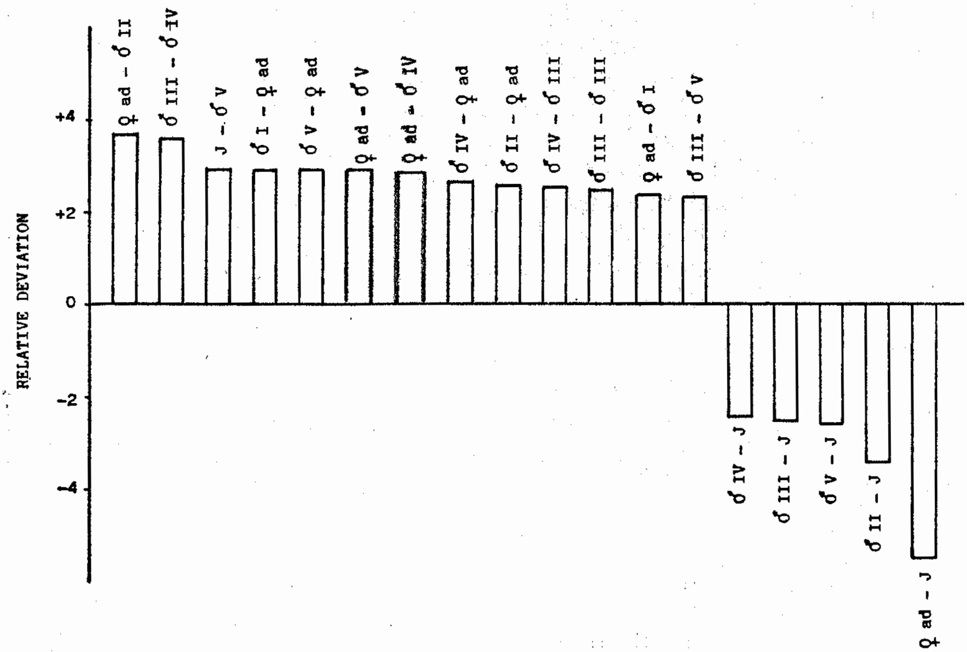

Fig. 6 : *Relative deviation* (Q_{ij}) *from the number of times that each pair of age/sex classes shown are expected to be together during the peak of the rut (1-15 Dec). All associations shown are statistically significant* ($P < 0.05$).

Fig. c: Ecart relatif (Q_{ij}) *par rapport au nombre de fois pour lequel chaque paire de classes d'âge et sexe devrait rester ensemble pendant le pic de la saison du rut (1-15 déc.). Toutes les associations présentées sont statistiquement significatives* ($p < 0.05$).

period in November and in *fig. 6* for the peak of the rut (1-15 December). These figures are based on a matrix with 80 degrees of freedom and the associations are statistically significant ($P < 0.05$). The results show that before the rut adult males associate only with other males of similar ages but sub-adult males, adult males and sub-adult females associate indiscriminately. There are negative associations between adult or subadult males and juveniles. During the peak of rut this negative association is maintained but there is a greater tendency for adult males and females to be found together, as would be expected.

DISCUSSION

The spatial distribution for animals within the group may be affected by several factors such as antipredator defence strategies, food competition and sociability among the group members. The social factors acquire a great importance during the rut, causing a change in the position of sex/age class members within the group. It is possible that outside the rut, adult males maximize their feeding competiveness by staying on the periphery of the group but during the rut, searching for mates is likely to be more important.

The greater cohesion of the group during the rut may be due to the males taking up positions in the the middle of the groups. At all times group cohesion is higher when the animal are feeding than when they are resting. This may be an antipredator strategy since feeding ibex are more likely to be visible to predators than are those lying down and a more cohesive grouping provides the usual benefits of greater predator detection and reduced individual vigilance.

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REFERENCES

Alados C.L., 1985a. Distribution and Status of the Spanish ibex (*Capra pyrenaica* Schinz). In : *The Biology and Management of Mountain Ungulates.* (ed. Lovari, S.), pp. 204-211. Croom-Helm. London.

Alados C.L., 1985b. Group size and composition of the Spanish ibex (*Capra pyrenaica* Schinz) in the Sierras of Cazorla and Segura. In : *The Biology and Management of Mountain Ungulates* (ed. Lovari, S.), pp. 134-147. Croom-Helm. London.

Alados C.L. 1986. Time distribution of activity in the Spanish ibex, *Capra pyrenaica. Biol. Behav. 11,* 70-82.

Altmann J., 1974. Observational study of behaviour : sampling methods. *Behaviour, 49,* 227-267.

Altmann S.A., Altmann J., 1977. On the analysis of rates of behaviour. *Anim. Behav. 25,* 364-372.

Clutton-Brock T.H., Greenwood P.J., Powell R.P., 1976. Ranks and relationships in highland ponies and highland cows. *Z. Tierpsychol., 41,* 202-216.

De Vore I., 1965. Male dominance and mating behavior in baboons. In : *sex and behavior* (ed. Beach, F.A.), pp. 266-290. New York : Wiley.

Eisenberg, J.F., Muckenhirn, N.A., Rudran R., 1972. The relation between ecology and social structure in primates. *Science, N.Y. 176,* 863-874.

Goss-Custard J.D., 1976. Variation in the dispersion of redshank *Tringa totanus* on their winter feeding ground. *Ibis, 118,* 257-263.

Hall M.J., 1983. Social organization in an enclosed group of red deer (*Cervus elaphus* L.) on Rhum. *Z. Tierpsychol. 61,* 272-292.

Hamilton, W.D., 1971. Geometry for the selfish herd. *J. Theor. Biol., 31,* 295-311.

Horn H.S., 1968. Adaptive significance of colonial nesting in the Brewer's Blackbird. *Ecology, 49,* 682-694.

Jennings T., Evans S.M., 1980. Influence of position in the flock and flock size on vigilance in the starling, *Sturnus vulgaris. Anim. Behav., 28,* 634-635.

Krebs J.R., 1973. Social learning and the significance of mixed-species flocks of chikadees (*Parus* ssp.). *Can. J. Zool., 51,* 1275-1288.

Rabenold K.N., Chistensen C.R., 1979. Effects of aggregation on feeding and survival in a communal wren. *Behav. Ecol. Sociobiol, 6,* 39, 44.

Robinson J.G., 1981. Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus. Anim. Behav., 29,* 1036-1056.

Walther F., 1977. Sex and activity dependency of distances between Thomson's gazelles (*Gazella thomsoni* Günther 1884). *Anim. Behav., 25,* 713-719.